able controversy about the significance between dominance rank, reproductive success, and genetic fitness among females."

We emphasized that the presence or absence of just one or two high-ranking females with reproductive pathology would influence perception of the significance of rank. We reported on five such females at Gombe and cited examples in other populations and species. While it is interesting that such rank-related pathologies have not yet been observed at Amboseli, there is no reason to dismiss them from our data set. A more productive approach would be to ask why such females might be more common at one site rather than another. Perhaps the historically high rate of infant mortality at Amboseli[4] has removed infertile animals from this population.

Altmann *et al.* suggest that, since field data cannot detect pregnancy for the first few days after conception, we may have missed many spontaneous abortions in the initial stages of pregnancy, and they predict that early abortions would be highest in low-ranking females. This prediction, however, is not confirmed by the Gombe data. If low-ranking females suffered a higher rate of undetected abortions immediately after implantation, they should take significantly more cycles to become obviously pregnant. However, once Gombe females resume cycling, there is no significant effect of rank on their interval to the next detectable pregnancy. Thus, early abortion is independent of rank at Gombe, and our miscarriage data are unbiased.

Further, we did not solely detect miscarriage on the basis of perineal coloration. Our analysis also included six miscarriages detected on the basis of delayed menstruation, and these all occurred in the first four weeks after conception (out of 50 miscarriages where the day of conception was known). There was no relationship between a female's rank and the gestation length of her failed pregnancy (t=0.52, P=0.6081, n=48 females of known rank). Our conclusion therefore remains unaltered: high-ranking Gombe females suffer more miscarriages, and this demographic pattern has been confirmed by Wasser[6] in a third baboon population.

We suggested that high-ranking females might show higher levels of androgens, as these have been implicated in the reproductive pathologies of several other mammalian females. The data presented by Altmann *et al.* are too limited to provide a rigorous test of this hypothesis. Most miscarriages at Gombe were suffered by females ranking fourth or higher, and Altmann *et al.* provide no data for any adult female ranked higher than sixth. Further, their data on androstenedione levels in juvenile females actually support our hypothesis. The regression of the log-transformed androstenedione levels on juvenile dominance rank is significantly positive (P=0.0470, n=6). Female dominance rank is established during the juvenile period and early exposure to androstenedione is believed to influence aggressiveness of adult females[17]. However, androgens are not the only hormones involved in aggressive behaviour, and competition may also be balanced by other physiological costs (see ref. 6). Further, reproductive pathologies at Gombe appear to be hit or miss — some high-ranking females have large numbers of surviving offspring whereas others have none. The most compelling data on reproductive failure would be from those specific adult females with some form of pathology.

The pattern in our miscarriage data does not result from our methodology. High-ranking females at Gombe and Mikumi[6] suffer significantly higher rates of miscarriage during detectable pregnancies. At Gombe, the greater incidence of reproductive pathology and the high miscarriage rate in high-ranking females essentially cancel the striking advantages of high rank from shorter post-partum amenorrhoea, higher infant survival and an earlier age of sexual maturation. These trends may or may not hold at all field sites, and contrasting results may prove useful in clarifying the costs and benefits of aggressive competition in different ecological settings. Although limited, the Altmann *et al.* data support our suggestion that female rank is correlated with androgen levels, androstenedione being highest in juvenile females of highest dominance rank. Wasser's[6] study of yellow baboons and findings by Frank *et al.*[18] on spotted hyaenas further emphasize the value of investigating the reproductive costs of aggressive competition in female mammals.

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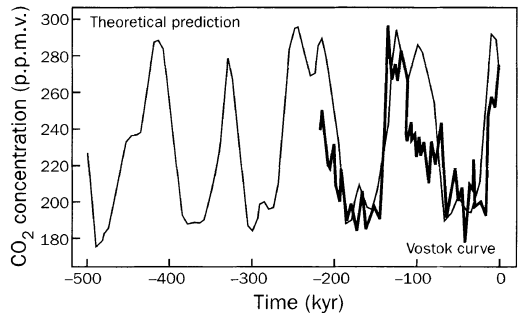
Predicting the Vostok CO_2 curve

SIR — To provide more than an *ad hoc* explanation of observed phenomena, a theoretical model must predict some as yet unobserved variability that places the model 'at risk' in some verifiable respect. In our phenomenological dynamical-system model governing changes in global ice volume, atmospheric CO_2 and the deep ocean state over the late Cenozoic[1,2], as influenced by Earth-orbital and slow tectonic CO_2 forcing, free parameters were assigned to account for the complex variations in global ice volume revealed by $\delta^{18}O$ proxy evidence. This includes internal bifurcations to the 'ice age' around 2.5 Myr ago and to the main near-100-kyr-period variations around 0.7 Myr ago. As a side consequence, the main features of the variations in CO_2 over the past 218 kyr were deduced and these compare favourably with those determined by the Vostok core trapped-air measurements[1–4].

As the drilling of the Vostok core is now projected to approach a depth corresponding to roughly 500 kyr ago[3], we now offer, as a further prediction of our model, the expected variation in CO_2 for the additional 300 kyr (see figure). According to the theory, the character of the variations should change somewhat, showing a shorter-period fluctuation, with new minima near 300 and 370 kyr ago. At present, this model is the only one from which such a prediction can be made as a response to purely external forcing, dealing with CO_2 as a free, internal, dynamic variable[5,6] rather than as a prescribed function (as in refs 7–9).



Variations over the Late Pleistocene of atmospheric CO_2 as inferred from the Vostok ice core[3] (heavy line) and from the dynamical theory[1,2,4] (thin line).

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